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Mitogenomics and the genetic differentiation of contemporary *Balaena mysticetus* (Cetacea) from Svalbard

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Full mitochondrial genomes were assembled for 12 recently sampled animals from the Svalbard bowhead whale (*Balaena mysticetus*) stock via high-throughput sequencing data, facilitating analysis of the demographic history of the population for the first time. The Svalbard population has retained noticeable amounts of mitochondrial genome diversity despite extreme historical harvest levels. Haplotype and nucleotide diversities were similar to those estimated earlier for other bowhead whale populations. The reconstructed demographic history was in accordance with a boom–bust scenario, combining a slight Pleistocene population growth 25 000–35 000 years ago and a Holocene decline. Employing a mutation rate of 3.418×10^{-8} substitutions per site per year, the time to the most recent common ancestor for the mitochondrial genomes of the contemporary Svalbard bowhead whales was estimated to be 68 782 (54 353–83 216) years before the present. Based on 370 bp fragments of the D-loop region, significant genetic differentiation was detected between all extant bowhead whale populations across the circumpolar Arctic. Thus, the Svalbard bowhead whales can be regarded as a population with its own genetic legacy.

ADDITIONAL KEYWORDS: baleen whales – bowhead whales – demographic history – evolutionary genetics – marine mammals – population differentiation – Spitsbergen stock – stock identity.

INTRODUCTION

Bowhead whales (*Balaena mysticetus* Linnaeus, 1758) occur in Arctic and subarctic regions. This species is the only baleen whale that exhibits such a high latitude distribution year-round. Four geographically isolated stocks (management units) have been recognized for this species by the International Whaling Commission (IWC), The International Union of Conservation of Nature (IUCN) and the North Atlantic Marine Mammal Commission (NAMMCO). They are: (1) the Bering/Chukchi/Beaufort Seas (BCB); (2) the Sea of Okhotsk (OKH); (3) the Baffin Bay/Davis Strait (BBDS) and Hudson Bay/Foxe Basin (HBFB) groups, which have recently been combined into Eastern Canada/West Greenland (ECWG); and (4) the Svalbard (Spitsbergen) stock, which is distributed in the Greenland Sea and the northern Barents Sea. There is, unfortunately, some inconsistency in the terminology in the literature referring to these different groups: the IWC and NAMMCO use the term

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'stock', which may be considered misleading because, traditionally, a stock refers to a geographically bounded, exploited part of a population, whereas IUCN uses the term 'subpopulation', when in reality little is known about the population structure of bowhead whales. In the current paper only 'population' is used in order to avoid confusion.

While there is already good knowledge about the distinction of the BCB, ECWG and OKH populations (see below), it is still uncertain, if the Svalbard population represents a meaningful biological entity, i.e. a diverging population with restricted gene-flow and neglectable migration over significant time periods. To answer this question, the population genetic structuring of this species needs to be addressed in greater detail. Key issues are: (1) to what extent have sea-ice barriers in the Arctic shaped patterns of genetic differentiation via preventing migration (gene flow) between populations and (2) to what extent is the history of extensive whaling reflected in their genetic structure. Answers to these questions are fundamental to improving the management of this species across the circumpolar Arctic.

The Svalbard bowhead whale population is currently classified as 'Endangered' by the IUCN (Cooke & Reeves, 2018). Extensive hunting, commencing in the early 17th century, drove this population from an estimated population size somewhere between 25 000 and 100 000 individuals (Allen & Keay, 2006) to commercial extinction. The population was believed to number in the tens in the early 1990s (Christensen *et al.* 1992). However, reliable population-size estimates may have been hampered by shifts of habitat use over large spatiotemporal scales. For example, a shift from use of open water to dense sea-ice in response to the presence of killer whales [*Orcinus orca* (Linnaeus, 1758)] has been recently reported for bowhead whales in the Canadian Arctic (Matthews *et al.*, 2020). When earlier attempts to survey bowhead whales in the Svalbard population from ships was replaced with a helicopter survey platform, in addition to ship-based effort, in 2015, the study area from the Russian border westward to North of the Svalbard Archipelago contained an estimated 350 bowhead wales, all sighted well within the margins of the ice edge (i.e. none were seen in open-water areas from the ship; Vacquié-Garcia *et al.*, 2017). Furthermore, there are a growing number of observations that suggest that the current size of the Svalbard population is larger than previously thought (Boertman *et al.*, 2009, 2015; de Boer *et al.*, 2019).

The first genetic study on population structure of Svalbard bowhead whales was based on bone material from 99 individuals (mainly from pre-whaling times) and targeted the molecular variance of 453 bp of the mitochondrial D-loop region (Borge *et al.*, 2007). The authors of this study reported high genetic diversity in the Svalbard population, and a slight but significant genetic differentiation between the ancient Svalbard and the contemporary BCB populations. However, Borge *et al.* (2007) did not consider the detected level of genetic differentiation between these datasets to be informative. They recommended caution in the interpretation of the results because both datasets had high proportions of low-frequency haplotypes. Furthermore, the Svalbard dataset did not result from a population survey but, instead, was a compilation of haplotypes spread over a period of ~50 000 years without homogeneous sampling over time.

Alter *et al.* (2012) provided the first comprehensive analyses of genetic differentiation of historic and contemporary bowhead whale populations. They focused on the genetic differentiation between the ECWG, BCB and OKH populations. However, they also included mitochondrial D-loop sequence data from Borge *et al.* (2007) in their analyses that were trimmed to a length of 370 bp. The study revealed small, but significant differentiation between the BCB and ECWG, and marked differentiation between OKH and all of the other populations. Alter *et al.* (2012) concluded that there has been high gene-flow between the BCB, ECWG and Svalbard bowhead whale populations in the recent past.

Two recent studies have reported full mitochondrial genomes (mitogenomes) for Svalbard bowhead whales. Nyhus *et al.* (2016) included eight contemporary samples collected in the Fram Strait during ship-based surveys in 2006 and 2010, and reported three different mitogenome sequences; one of them found in six individuals that were sampled from a group of whales on the same day in the same area. Grond *et al.* (2019) studied ten heterochronous ancient bowhead whale samples collected from elevated beaches within the Svalbard Archipelago and provided ten full mitogenomes, the oldest dated to be 8885 years old (using ^{14}C). However, due to small sample-sizes, and a lack of similar data for the other populations, little could be concluded regarding the genetic identity of the Svalbard bowhead whale population based on these mitogenomes.

In this study, mitogenomes for 12 additional Svalbard bowhead whales collected during 2017 and 2018 are provided, increasing the available contemporary mitogenome dataset from eight to 20 for this population. This is still a low sample-size for genetic investigations, but the low number of available samples puts a premium on any information that can be gleaned from existing material. Herein, the genetic data for the contemporary Svalbard bowhead whales are compared with other populations, and genetic structure is discussed in a circumpolar context, with particular emphasis on demographic history and population differentiation.

MATERIAL AND METHODS

Skin biopsies were collected from 12 bowhead whales in the drifting pack-ice in the Fram Strait (Table 1) using a crossbow with custom-made arrows that have a biopsy dart at the tip (4 cm long; 8 mm diameter). The whales were approached from the air with a helicopter (Eurocopter AS350 Écureuil) and darted from a distance of 6–10 m. The dart bounced off the whale after the hit and floated at the surface, where it was subsequently collected with a small hoop net attached to a telescopic pole, while hovering close to the surface above it. Back at the ship (RV *Lance* in 2017 and RV *Kronprins Haakon* in 2018), the skin samples were frozen at –20 °C until analysis. Permits for animal handling were issued by the Norwegian Animal Research Authority (FOTS ID: 11821), the Governor of Svalbard (Sysselmannen, permit ID: 16/01600-6) and the Greenland Ministry of Fisheries, Hunting and Agriculture (ref. 2017–2551, akt. no.8267820).

Total genomic DNA was extracted using the E.Z.N.A. Tissue DNA kit (Omega Bio-Tek) following the Tissue DNA-Spin Protocol. Preparation of paired-end libraries and analysis on an Illumina NextSeq 500 (read length 150 nucleotides) was outsourced to StarSEQ GmbH, Mainz, Germany. The raw reads obtained were first quality trimmed (TrimGalore v.0.3.3., https://www.bioinformatics.babraham.ac.uk/projects/trim_galore/). Subsequently, the mitogenomes were assembled using MITObim v.1.8 (Hahn *et al.*, 2013). GenBank entry AJ554051, a full mitogenome sequence from a bowhead whale sample collected in West Greenland (Arnason *et al.*, 2004), was used as reference sequence. Both applications were used with default parameters. Molecular sexing was also done using MITObim v.1.8 (Hahn *et al.*, 2013) with the ZFX/ZFY gene sequences (Berube & Palsbøll, 1996) as reference. The raw mitochondrial reads (as identified by MITObim v.1.8) and the assembled mitogenome sequences have been deposited in NCBI's Sequence Read Archive (SRA; Bioproject: PRJNA643010) and in GenBank (accession numbers are listed in Table 1), respectively.

DnaSP v.6.12.03 (Rozas *et al.*, 2017) was employed to estimate genetic diversity statistics including the number of haplotypes (k), the number of segregating sites, haplotype (H_D) and nucleotide (π) diversity as well as Tajima's D. Arlequin suite v.3.5 (Excoffier & Lischer, 2010) was used to address genetic population differentiation by means of fixation index F_{ST} (using haplotype frequencies and Reynold's distances with 100 repetitions) and exact tests (Raymond & Rousset, 1995) with 100 000 Markov chain runs and 10 000 dememorization steps. Population-specific datasets were compiled for three mitochondrial markers. Dataset 1 included: the 957 bp NADH dehydrogenase 1 (*ND1*) gene sequences of 168 BCB (Phillips *et al.*, 2013), ten ancient Svalbard (Grond *et al.*, 2019) and 20 contemporary Svalbard (Nyhus *et al.*, 2016; this study) samples. Dataset 2 included: a 458-bp fragment of the cytochrome *b* (*Cytb*) gene of 102 ECWG (McLeod *et al.*, 2012), 168 BCB (Phillips *et al.*, 2013), 63 OKH (Meschersky *et al.*, 2014), ten ancient Svalbard (Grond *et al.*, 2019) and 20 contemporary Svalbard (Nyhus *et al.*, 2016; this study) samples. Dataset 3 included nucleotide sequences of the mitochondrial D-loop, hitherto the most commonly used molecular marker for addressing genetic differentiation of bowhead whale populations: a 370-bp fragment as defined by Alter *et al.* (2012) of 264 ECWG (Alter *et al.*, 2012), 168 BCB (Phillips *et al.*, 2013), 96 BCB (Rooney *et al.*, 2001), 63 OKH (Meschersky *et al.*, 2014), 100 ancient Svalbard (Borge *et al.*, 2007; Grond *et al.*, 2019) and 20 contemporary Svalbard (Nyhus *et al.*, 2016; this study) samples. In all analyses, ancient and contemporary Svalbard samples combined were also included.

An unrooted haplotype network and a maximum likelihood (ML) phylogram were used to illustrate the relationships between the contemporary mitochondrial haplotypes. The unrooted haplotype network was constructed based on the statistical parsimony method (Templeton *et al.*, 1992) using the haploNet function, implemented in the pegas package (Paradis, 2010) in R (R-Development Core Team, 2016). Maximum likelihood analyses were carried out in PHYML v.3.0 (Guidon *et al.*, 2010) applying the GTR model as selected by the SMS option of the program (Lefort *et al.*, 2017). The mitogenome sequences of the southern right whale [*Eubalaena australis* (Desmoulins, 1822), NC_006930] and the North Pacific right whale [*E. japonica* (Lacépède, 1818), NC_006931] served as outgroups. Bootstrap support values were estimated using 1000 replicates.

The demographic history of the Svalbard bowhead whale population based on the 20 available contemporary and ancient mitogenomes was inferred using the Bayesian skyline plot method (Drummond *et al.*, 2005) implemented in BEAST v.2.6.0 (Bouckaert *et al.*, 2014). For the aligned mitogenomes, 38 regions, including protein-coding (PCG), rRNA and tRNA genes, as well as the control region (CR), were individually extracted based on published coordinates and assigned to six partitions: (1) first-, (2) second-, (3) third-codon position of the PCG, (4) tRNA, (5) rRNA genes and (6) the CR. The best-fit partitioning schemes and substitution models for the six partitions (Supporting Information, Table S1) were identified using the corrected Akaike information criterion with PartitionFinder v.2.1.1 (Lanfear *et al.*, 2017). The six partitions were analysed using unlinked substitution models, but linked genealogy and molecular clock. Six groups of coalescent intervals and a strict molecular clock

Table 1. Spitsbergen bowhead whale samples included in this study

Sample ID	Date/^{14}C age (years)	sex	Latitude	Longitude	mt reads	Coverage (ca x)	Haplotype*	GenBank accession no	SRA accession no
Novel contemporary mitogenomes (this study)									
17-05	03.06.17	male	76.53N	3.54W	262,917	2,300	III	MT649195	SAMN15402837
17-07	04.06.17	female	76.41N	4.14W	378,629	3,300	IV	MT649187	SAMN15402838
17-08	04.06.17	male	76.41N	4.14W	398,550	3,400	V	MT649194	SAMN15402839
17-10	04.06.17	female	76.34N	3.28W	292,632	2,550	VI	MT649188	SAMN15402840
17-12	04.06.17	female	76.35N	3.36W	368,606	3,200	V	MT649193	SAMN15402841
17-17	05.06.17	male	76.34N	3.20W	439,983	3,800	VI	MT649189	SAMN15402842
17–18	05.06.17	male	76.29N	2.33W	510,808	4,450	VII	MT649190	SAMN15402843
17–19	08.06.17	male	76.50N	4.30W	427,376	3,700	I	MT649196	SAMN15402844
17–20	08.06.17	female	76.50N	4.30W	363,514	3,200	VIII	MT649191	SAMN15402845
17–21	08.06.17	male	76.50N	4.31W	549,888	4,800	IX	MT649192	SAMN15402846
18-05	31.08.18	male	79.17N	18.25W	143,095	1,200	I	MT649185	SAMN15402847
18-06	31.08.18	male	79.17N	18.25W	254,478	2,100	II	MT649186	SAMN15402848
Contemporary mitogenomes (Nyhus *et al.* 2016)									
A	18.04.06	female	80.58N	2.09E		1,515	III	KY026766	
B	18.04.06	female	80.58N	2.09E		1,712	III	KY026767	
C	18.04.06	female	80.58N	2.09E		2,074	III	KY026768	
D	18.04.06	female	80.58N	2.09E		2,054	III	KY026769	
E	18.04.06	female	80.58N	2.09E		1,033	III	KY026770	
F	18.04.06	female	80.58N	2.09E		3,028	III	KY026771	
H	26.04.06	female	81.04N	1.16E		117	V	KY026773	
I	03.04.10	female	79.54N	1.03E		212	IV	KY026772	
Ancient mitogenomes (Grond *et al.* 2019)									
NHMO-DMA-43194	215		77.40N	22.30E		50		MN124685	SRR9937203
NHMO-DMA-43195	325		77.40N	22.30E		127		MN145937	SRR9937202
NHMO-DMA-43197	325		77.00N	21.55E		14.5		MN145938	SRR9937201
NHMO-DMA-43191	370		77.10N	21.00E		8		MN145939	SRR9937200
PMO 234.573	375		78.38N	11.55E		10		MN159080	SRR9937199
PMO 234.423	405		78.38N	11.55E		12		MN159085	SRR9937198
NHMO-DMA-43206	415		78.19N	18.55E		37		MN159084	SRR9937197
PMO 234.525	990		76.56N	15.46E		14		MN159083	SRR9937196
PMO 234.429	7,380		78.43N	15.29E		10		MN159082	SRR9937205
PMO 234.522	8,885		78.26N	16.31E		13		MN159081	SRR9937204

* as depicted in Figure

were assumed. Details of the analyses are provided as Supporting Information, File S1. Posterior distributions of parameters were estimated using Markov chain Monte Carlo (MCMC) sampling with 100 million burn-in steps followed by 1000 million steps, sampled at every 100 000 steps. Convergence to stationarity and mixing across chains were assessed using TRACER v.1.7.1 (Rambaut & Drummond, 2018). A minimum effective sample-size of 5000 was required for all parameter estimates.

A mutation rate for the bowhead whale mitogenomes was inferred using BEAST v.2.6.0 (Bouckaert *et al.*, 2014). The resulting mutation rate was 3.418×10^{-8} [95% HPD (highest posterior density): 1.35×10^{-8}–5.63×10^{-8}] substitutions per site per year.

RESULTS

Read numbers and coverage of the successful assembly of 12 mitogenomes from Svalbard bowhead whale samples collected in 2017 and 2018 are summarized in Table 1. The novel mitogenomes are 16 389–16 391-bp long with indels occurring in the 12S and 16S genes and in the noncoding CR. The alignment with earlier published mitogenomes of other Svalbard bowhead whale individuals is straightforward (Supporting Information, File S2). Among the 12 novel mitogenomes in this study, there are a total of nine different haplotypes, three of which occur in two samples each.

Among the 20 mitogenomes from the contemporary Svalbard bowhead whales, there are 142 variable sites (138 transitions, two transversions and three indels) across the nine haplotypes. The average nucleotide diversity is $\pi = 0.0027$. In this expanded dataset, 106 substitutions affecting protein-coding regions (86 synonymous and 20 non-synonymous substitutions), seven RNA genes and 25 noncoding positions occur. Additional genetic diversity parameters for the contemporary mitogenomes are summarized in Table 2. It is noteworthy that Tajima's D, i.e. the difference between the mean number of pairwise differences and the number of segregating sites, is not significant. In terms of nucleotide diversity, the noncoding CR is the most diverse region ($\pi = 0.00853$), while among the protein-coding genes, *ND5* is the most ($\pi = 0.00445$) and *COI* is the least ($\pi = 0.00036$) diverse (Supporting Information, Table S2). The haplotype network depicted in Figure 1 illustrates the relationships among the contemporary Svalbard bowhead whale mitogenomes. A similar grouping of haplotypes is depicted in the ML phylogram (Supporting Information, Fig. S1).

The Bayesian skyline plot (Fig. 2) illustrates the demographic history of the Svalbard bowhead whale population based on the 20 contemporary and the ten ancient mitogenomes. There is a slight increase in genetic diversity (Θ) during the Pleistocene 25 000–35 000 years ago (for details see also: Supporting Information, File S3). Such increase in Θ might be due to, for example, population expansion, increased migration and gene flow or, most likely, a combination of various parameters. In addition, the Bayesian skyline plot shows a strong decline in Θ during the Holocene. Assuming no changes in gene flow through time, the mean of the effective population size for females [$N_{e(female)}$] increased during the Pleistocene from about 70 000. to about 110 000. However, the confidence limits are broad and overlapping throughout the time frame. The time to the most recent common ancestor (MRCA) for the 20 contemporary mitogenomes was estimated to be 68 782 (54 353–83 216) years before the present, employing a mutation rate of 3.418×10^{-8} substitutions per site per year. For the dataset including both the contemporary and the ancient mitogenome sequences, the MRCA was estimated to be 75 278 (33 450–133 380) years before present.

Analyses of genetic differentiation of bowhead whale populations were performed with three datasets, and the results are summarized in Table 3. Using 957 bp *ND1* sequences (dataset 1), there was no significant F_{ST} between the BCB and the ancient or contemporary Svalbard populations. However, the exact test, based on haplotype frequencies, indicates significant differentiation between the ancient and contemporary Svalbard populations. For the 458 bp *Cytb* sequences (dataset 2), genetic differentiation was detected when comparing the OKH samples to all the other populations and also when comparing the Svalbard samples with the BCB and ECWG datasets.

Table 2. Genetic diversity of contemporary mitochondrial genomes of Svalbard bowhead whales

N	bp	GM	S	η	SVS	PIS	*h*	H_D (SD)	π	Tajima's D
20	16 392	3	139	140	17	122	9	0.858 (± 0.061)	0.0027	0.469 ($P > 0.1$)

The estimates are based on an analysis of the 12 mitogenomes presented in this study and eight mitogenomes reported earlier by Nyhus *et al.* (2016). They include the number of sequences per dataset (*N*), the length of the alignment in base pairs (bp), the number of gaps and missing data (GM), the number of segregating (polymorphic) sites (S), the total number of mutations (η), the number of singleton variable (SVS) and parsimony informative sites (PIS), the number of haplotypes (*h*), the haplotype diversity (H_D) with the standard deviation (SD), the nucleotide diversity (π) and Tajima's D.

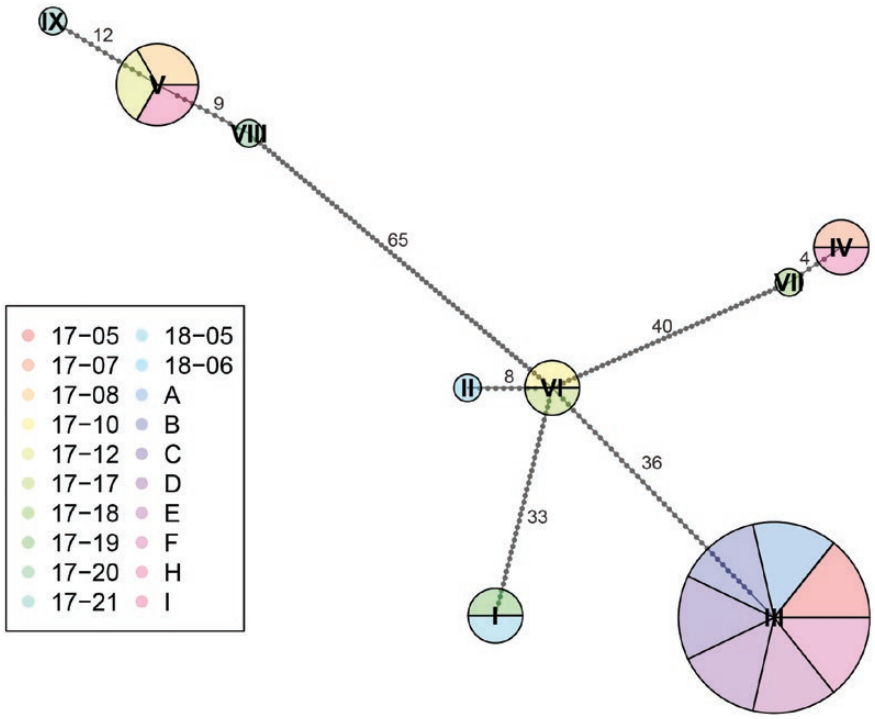

Figure 1. Haplotype network of complete mitogenomes of 20 contemporary Svalbard bowhead whales. Each circle represents a distinct haplotype (I–IX). Circle sizes reflect the number of specimens sharing a haplotype. Numbers and black dots indicate the number of variable sites between haplotypes. Samples A–I are taken from Nyhus *et al.* (2016).

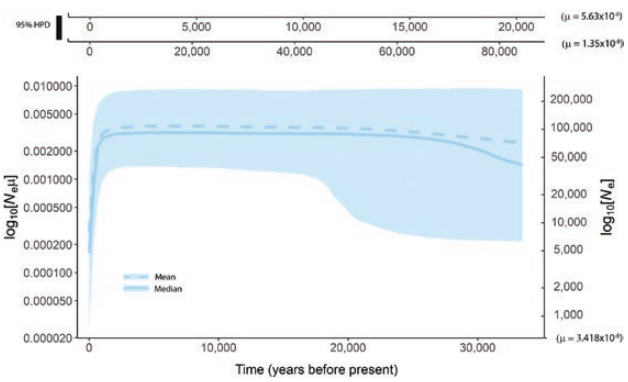

Figure 2. Bayesian skyline plot illustrating the temporal changes in the genetic diversity of mitogenomes in Svalbard population bowhead whales. The top of the figure illustrates the time in years before present when using the 95% HPD interval of the estimated divergence time for the calculation of μ.

Furthermore, the ancient and the contemporary Svalbard datasets differed significantly from one another. For the 370 bp D-loop fragments (dataset 3), significant differentiation was detected for most comparisons. The only exceptions were the pairwise comparisons of the combined ancient and contemporary Svalbard samples with either the BCB samples from Phillips *et al.* (2013) in F_{ST} or the BCB samples from Rooney *et al.* (2001) in the exact test.

DISCUSSION

For the 20 bowhead whale mitogenomes from the contemporary Svalbard population, the overall genetic variation in terms of haplotype diversity (H_D = 0.858) and nucleotide diversity (π = 0.0027) is somewhat lower than most earlier estimates reported for bowhead whales (for an overview see: Supporting Information, Table S2), as well as for other species, e.g. the humpback whale (*Megaptera novaeangliae* Borowski, 1781) with H_D = 0.985 and π = 0.021 for the CR of a global dataset (Jackson *et al.*, 2014) or the southern right whale (*Eubalaena australis*) with H_D = 0.913 and π = 2.68 for the CR of a Southern Hemisphere dataset (Rosenbaum *et al.*, 2000). Among bowhead whales, lower values have been reported only for OKH. However, it is noteworthy that extended mitogenome data are only available for the Svalbard population, and haplotype diversity estimates for the other populations have mostly been reported from the analyses of short stretches of the CR. Since these earlier estimates are based on the fastest evolving

Table 3. Genetic differentiation of bowhead whale populations

Population	SS ancient	SS contemp.	SS combined	CCA	EA-WG	BCB1	BCB2	OKH
NADH1 (*ND1*) gene (dataset 1)								
SS ancient		0.0437	-0.0278			-0.0195		
SS contemp.	**0.0460**		-0.0198			0.0281		
SS combined	0.3606	1				0.0087		
CCA								
EA-WG								
BCB1	0.1672	0.9740	0.6341					
BCB2								
OKH								
Cytochrome *b* (*Cytb*) gene (dataset 2)								
SS ancient		0.0857	0.0021	-0.0129		-0.0353		**0.2350**
SS contemp	**0.0248**		-0.0231	**0.1818**		**0.0996**		**0.4791**
SS combined	0.4022	0.9629		**0.1065**		**0.0411**		**0.3663**
CCA	0.1854	**0**	**0.0012**			0.0116		**0.0944**
EA-WG								
BCB1	0.3483	**0.0026**	**0.0105**	0.0672				**0.1505**
BCB2								
OKH	**0.0001**	**0**	**0**	**0.0001**		**0**		
Control region (CR) – D-loop (dataset 3)								
SS ancient		**0.0333**	-0.0082		**0.0194**	0.0034	**0.0156**	**0.0464**
SS contemp.	**0.0293**		0.0167		**0.0893**	**0.0290**	**0.0285**	**0.0908**
SS combined	0.5890	1			**0.0239**	0.0029	**0.0140**	**0.0465**
CCA								
EA-WG	**0**	**0**	**0**			**0.0343**	**0.0642**	**0.0834**
BCB1	**0.0008**	**0**	**0**		**0**		**0.0141**	**0.0458**
BCB2	0.1057	**0.0034**	**0.0002**		**0**		**0.0060**	**0.0783**
OKH	**0**	**0**	**0**		**0**	**0**	**0**	

Pairwise F_{ST} estimates (above diagonal) and exact test results (*P*-values, below diagonal) based on haplotype frequencies are indicated. Significant genetic differentiation (significance level $\alpha = 0.05$) is marked in bold.
SS ancient: Svalbard population ancient samples (Borge *et al.*, 2007; Grond *et al.*, 2019).
SS contemp: Svalbard population contemporary samples (Nyhus *et al.*, 2016; this study).
SS combined: Svalbard population ancient and contemporary samples combined.
CCA: Central Canadian Arctic (McLeod *et al.*, 2012).
EA-WG: Eastern Canada-West Greenland (Alter *et al.*, 2012).
BCB1: Bering/Chukchi/Beaufort Seas (Phillips *et al.*, 2013).
BCB2: Bering/Chukchi/Beaufort Seas (Rooney *et al.*, 2001).
BCB1 and BCB2 may to some extent include the same samples.
OKH: Okhotsk Sea (Meschersky *et al.*, 2014).

part of the mitogenome, it is not surprising that haplotype diversity estimates based on protein-coding sequences are lower (Supporting Information, Table S2). The haplotype and nucleotide diversity values reported here for the mitogenomes of contemporary Svalbard bowhead whales may, to some extent, reflect the low sample-size and a potential sampling bias. Six of the eight samples collected in 2006 with identical mitogenome sequences were taken on the same day in the same area from a group of animals. Although speculative, it cannot be excluded that these samples represent a matriline of closely related individuals. However, to our knowledge it has never been reported that bowhead whales actually travel in such hypothetical family groups, although there are certainly reports of females travelling in groups with calves and young whales (e.g. Southwell, 1898; Reeves *et al.*, 1983).

Extensive commercial hunting of bowhead whales immediately following the discovery of the Svalbard Archipelago, in which Spitsbergen is the largest island, in the early 17th century drove the Svalbard bowhead whale population almost to extinction. Although lower than values reported for most other populations, the small remaining Svalbard population appears to have retained noticeable amounts of haplotype and nucleotide diversity, which indicate that the population still harbours modest levels of mitogenome diversity. This is corroborated in the current study by the minimum spanning network and the ML phylogram. Both analyses reveal the presence of several mitogenome lineages, and the time

to the MRCA for the mitogenomes is estimated to be roughly 70 000 years. In line with Foote *et al.* (2013), this study concludes that the mitochondrial lineages of the Svalbard population survived Late Pleistocene climate changes.

The 20 complete contemporary mitogenomes made it possible to analyse the demographic history of the Svalbard bowhead whale population for the first time. The changes in genetic diversity (Θ) that have taken place through time are compatible with a boom–bust scenario, combining a slight Pleistocene population growth 25 000–35 000 years ago and a Holocene decline. Under the assumption of no gene-flow over time, the Pleistocene growth would have been the result of an increased effective population-size for females [$N_{e(female)}$] from ~70 000 to ~110 000. However, the confidence limits are broad and overlapping throughout the time frame and thus the estimates have to be interpreted cautiously. Nevertheless, these numbers seem reasonable when compared to estimates of pre-exploitation population size of around 52 500 individuals with a plausible range of 25 000 to 100 000 individuals in the Svalbard bowhead whale population (Allen & Keay, 2006). The results obtained for the demographic history of the Svalbard population are also corroborated by those obtained for the BCB population by Phillips *et al.* (2013). Their demographic reconstructions included data for 324 (22 microsatellite loci) and 164 (mitochondrial D-loop sequences) samples and indicated an increase in $N_{e(female)}$ between 50 000 and 75 000, followed by a population reduction approximately 15 000 years ago. Phillips *et al.* (2013) concluded that the inferred demographic changes coincided with glacial periods and the onset of warming at the end of the last glacial maximum, respectively. McLeod *et al.* (2012) addressed potential historical changes in distribution and connectivity of bowhead whales across the Canadian Arctic Archipelago. These authors analysed mitochondrial DNA sequences from 106 ancient bowhead whale samples ranging in age from 471 to 10 290 years BP and found low differentiation when comparing the data with the Holocene Svalbard and contemporary BCB populations. In addition, they detected signals of population expansions over the past 30 000 years. They concluded that either the long generation-time of bowhead whales, occasional population connectivity, a historically large global population or a combination of these parameters might explain the results. The skyline plot of Cabrera *et al.* (2018), based on D-loop sequences, also showed a historical, although more recent, population expansion dated to ~15 000 years ago for ECWG bowhead whales, an estimate that falls within the 95% HPD of the estimate for the Svalbard population. However, for the ECWG population, there was no signal for a Holocene decline, most likely because the authors excluded the last 1000 years from their analyses. Foote *et al.* (2013) studied D-loop sequences from 15 Late Pleistocene bowhead whale samples collected from Sweden and Denmark, both regions where the species no longer occurs today. These authors also report a rapid increase in effective female population-size beginning ~40 000 years ago, which they relate to an assumed threefold increase in core suitable habitat. The demographic patterns for the recognized bowhead whale populations are all in accordance with a boom–bust scenario, with a Late Pleistocene boom in genetic diversity (interpreted as an increase in population size) reported in all studies, and a consistent pattern of a Holocene bust in studies that included contemporary samples in the analyses. The differences in the details in the various studies might be due to differences in the methods used for the analyses, the applied parameters, e.g. mutation and/or migration rates between populations, and differences in sample sizes.

There has been an extensive debate as to whether the recognized bowhead whale populations (or subpopulations) reflect biological entities or just geographically defined management units. Over the years, several reports have been submitted to the International Whaling Commission regarding this issue (e.g. Alter *et al.* 2008; Bachmann *et al.* 2008; Gavrilo 2015). Bowhead whales are tightly associated with sea ice, and the key question in this context is to what extent migration between populations has been restricted by periods with extensive sea-ice, and how such barriers might have shaped population structure over time. It is assumed that bowhead whales moved into the Arctic Ocean via the Bering Strait some 10 000 years ago (Dyke & Savelle, 2001), concomitant with an increase in temperature and reduction in sea-ice cover that were coincident with accelerated deglaciation rates at the Pleistocene–Holocene transition (Clark *et al.*, 2009). The resulting overall increase in primary productivity caused an initial expansion of baleen whales in the Northern Hemisphere either immediately after the Last Glacial Maximum (LGM; 19 000–26 000 years ago) or later during the initial phase of the Pleistocene–Holocene transition (Cabrera *et al.*, 2018). The ECWG bowhead whale population is thought to have originated either from the BCB or from the Svalbard population (Dyke *et al.* 1996). Alternatively, there has been a suggestion that the Svalbard population originated from a refugial population that occupied the eastern North Atlantic (Fredén, 1975). Inter-ocean connectivity may have allowed, at least for limited periods, migration between populations. According to Dyke & Savelle (2001), migration between Pacific and Atlantic bowhead whale populations was unrestricted 8500–10 000 years ago, while it is thought that the M'Clintock

Channel sea-ice plug likely prevented migration until 3000–5000 years ago between the Pacific and North-Atlantic populations (Dyke *et al.*, 1996).

There is general agreement that OKH is genetically differentiated from all other bowhead whale populations (Alter *et al.*, 2012; Meschersky *et al.*, 2014), which was corroborated by this study. The relationships of the other populations are much less conclusive, with conclusions regarding population identities/differentiations varying between studies. The first comprehensive study on the topic by Alter *et al.* (2012) revealed small but significant differentiation between the BCB and ECWG populations. Similarly, Borge *et al.* (2007) reported differentiation between the BCB and the ancient Svalbard population. However, all of these studies suffer from shortcomings in their datasets: (1) analyses relied mostly on mitochondrial sequences with little attention to nuclear genome data, (2) usually only short stretches of the mitochondrial control region were used and (3) data were not obtained from population surveys, but they were compiled from individual samples that arise from animals that lived during various time periods. The current study on contemporary Svalbard mitogenomes also suffers from some of the aforementioned shortcomings, most importantly low sample-size and the potential for having sampled related individuals of the same matriline. Nevertheless, it includes an expanded set of novel, contemporary Svalbard population samples in the analyses. Using this novel dataset, significant genetic differentiation was detected between all extant bowhead whale populations. Accordingly, the Svalbard bowhead whales should be regarded as a population with its own genetic legacy. The unique diversity of songs recorded by Stafford *et al.* (2018) in the Fram Strait is supportive of this interpretation.

Foote *et al.* (2013) explained the shallow genetic differentiation of bowhead whale populations. Based on only limited sequence data from few samples, these authors postulated that Holocene populations reoccupied Arctic waters from more southerly waters either in the Atlantic, the Pacific or both, after the LGM. Assuming a substitution rate of 2×10^{-7} substitutions per site per year (Ho *et al.*, 2007), a rate that is close to the upper 95% HPD bound of the estimate used in this study, and a separation of populations lasting approximately 10 000 years, there would only have been sufficient time to generate a small genetic differentiation between the populations.

It is noteworthy that cases of movement of individual bowhead whales between the ranges of recognized populations have never been reported. Theoretically, tracking with satellite transmitters allows for the detection of such movements. Hundreds of bowhead whales have been tracked, but all individuals have remained within the expected population ranges until recently (e.g. Heide-Jørgensen *et al.*, 2006; Ferguson *et al.*, 2010; Lydersen *et al.*, 2012; Citta *et al.*, 2015, 2018; Kovacs *et al.*, 2020). However, one individual from ECWG and one from BCB did enter the North-West Passage in 2010 from opposite directions (Heide-Jørgensen *et al.*, 2011). Although the study did not demonstrate actual migration between populations, it documented the potential for overlap between the two populations in summer, now that the Arctic sea-ice extent has declined so markedly. Increasingly, reduced sea-ice coverage arising from global warming might facilitate more frequent long-range movements of bowhead whales and, potentially, breeding between animal from previously isolated populations. However, this species has a strong sea-ice affiliation that may be intensified by the presence of killer whales, so more open-water may not automatically result in longer migration paths (Matthews *et al.*, 2020). Fidelity to population-specific, winter-breeding areas is also likely to slow genetic mixing.

CONCLUSIONS

Using the novel dataset presented here, significant population differentiation was detected between all extant bowhead whale populations. Accordingly, the Svalbard bowhead whales should be regarded as a population with its own genetic legacy and should be managed as a separate entity. Demographic reconstructions for all recognized bowhead whale populations suggest a common pattern of increased genetic diversity during the Late Pleistocene, although this trend is not compelling for the Svalbard population given the broad confidence interval of the estimate. The limited genetic differentiation between the currently recognized bowhead whale populations across the circumpolar range of the species has likely accumulated since the separation of the populations after the LGM. Accordingly, the question to what extent sea-ice barriers in the Arctic may have shaped patterns of genetic differentiation via preventing migration (gene flow) between bowhead whale populations seems to be of minor importance. Furthermore, one would also not yet expect the history of extensive whaling to be reflected markedly in the genetic structure of the species.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's web-site.

File S1. Details on the BEAST analysis of the Svalbard population bowhead whale mitogenomes.
File S2. fasta formatted alignment of the Svalbard bowhead whale mitogenomes.
File S3. Results of the BEAST analysis of population demography.
Figure S1. Maximum likelihood tree of mitogenome sequences from 20 contemporary Svalbard bowhead whales.
Table S1. Data partitions and best-fitting substitution models.
Table S2. Compilation of mitochondrial genetic diversity estimates of bowhead whale samples across studies.